CONTRIBUTIONS FROM THE ZOÖLOGICAL LABORATORY OF THE MUSEUM OF COMPARATIVE ZOÖLOGY AT HARVARD COLLEGE, UNDER THE DIRECTION OF E. L. MARK. — No. 113.

No. 11. — PERIPHERAL DISTRIBUTION OF THE CRANIAL NERVES OF SPELERPES BILINEATUS.

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Contents.

A. Introduction.

The study of the distribution of the cranial nerves of Spelerpes bilineatus was undertaken merely as introductory to an intended investigation of the central origin of the nerves; but it has seemed advisable to make this study more careful and detailed than was at first contemplated, and as a result the nerve roots have as yet been but superficially examined.

By studying the "components" of the individual nerves, following in

some degree the method adopted by Strong ('95), it has seemed possible to make out more accurately the homologies of Urodelan and Anuran nerves than has before been done.

The color scheme used by Strong has been followed as closely as practicable; roots and ganglia, however, have been left neutral from lack of knowledge of the exact proportions of the different components passing through the ganglia. Strong's nomenclature has also been adopted, since it proves quite as applicable to the Urodelan as to the Anuran type. The confusion which would have arisen from the use of two or more sets of terms is thus avoided.

My work has been carried on in the Radcliffe College Laboratory at the Museum of Comparative Zoölogy, Cambridge; and it is with great pleasure that I acknowledge here my indebtedness to the Director of the Laboratory, Professor E. L. Mark, who has assisted and advised me, and helped me in many ways. I also wish to express my sincere thanks to Dr. Harris H. Wilder and Dr. B. F. Kingsbury, who have kindly preserved and sent to me all my Spelerpes material.

B. Methods.

Several methods of preservation and staining were tried, but the material preserved in four per cent formalin and stained with Heidenhain's iron haematoxylin was the most satisfactory. The decolorizing process was stopped at the moment when the other tissues had given up their stain but the nerves still retained the deep blue color imparted to them by the haematoxylin. It was in this way that the series which served for the reconstructions were made. The sections were cut parallel to the sagittal plane through the left half of the head of a larva 23 mm. long, and were 20 μ thick. Figures 1 and 3, representing the nerves of the left side as projected on the sagittal plane, were made by outlining the accurately superposed images of the successive sections given by an Abbé camera. To insure the proper superposition, direction planes were employed. Before sectioning, the paraffine block was cut in prismatic form, the bounding planes being perpendicular to the prospective plane of sectioning; the faces of the prism were painted with a mixture of lamp-black and turpentine; the block was then quickly immersed in rather soft paraffine and again trimmed before sectioning. The rim of black around each section afforded a satisfactory means of accurate superposition.

Figures 2 and 4, representing projections on the frontal plane, were constructed from the same series, by plotting on millimetre paper the positions of the nerves as they occurred in the successive sections.

C. Eye-muscle Nerves, III., IV., and VI. (Pl. 2, Figs. 3, 4).

It was my intention to confine my work to the fifth, seventh, ninth, and tenth nerves, but in my examination of the ophthalmic branch of the trigeminus it became necessary to make a study of the eye-muscle nerves, from which some facts of interest were established. I therefore give a brief account of these nerves, — the third, fourth, and sixth cranial nerves.

The *oculomotor* (III.) arises, as usual, from the floor of the mesencephalon, passes through the brain wall, and then, lying between that wall and r. ophthalmicus V. (*V. opt.*), immediately gives off its r. superior (Pl. 2, Figs. 3, 4, III. *rt. su.*) to m. rectus superior. It then passes under r. ophthalmicus V., — which takes a more median position (Fig. 4), — and here lies for a short distance in close contact with a branch of the abducens (VI.) In some series of sections the two nerves, while indistinguishable on one side of the head, were clearly separable on the other. There is, then, no real fusion of the two.

A cluster of ganglion cells (*cl. gn.*) is constantly found enveloping that portion of the oculomotorius that lies directly ventrad to the optic nerve (see Figs. 3, 4). In the 23 mm. stage these ganglionic cells are grouped into a compact mass, but in older stages (40 mm.) they are somewhat scattered along the nerve. The oculomotorius follows closely m. inferior rectus, giving fibres to it, and ends in m. inferior obliquus.

The *trochlearis* (IV., Pl. 2, Figs. 3, 4) is very minute, and its whole course was not traceable in the 23 mm. stage; but in older larvae an interesting condition was observed. At the posterior margin of the eyeball this nerve joins a dorsal branch of r. ophthalmicus (*Va*), and the two run along the median dorsal surface of the eyeball to near its anterior margin as one nerve. Here the fibres of the trochlearis (*IV. ob. su.*) pass ventrad and are distributed to the superior oblique muscle; this ophthalmic branch of the fifth (*Va*) then passes forward and dorsad to innervate the skin in the regions in front of the eye. Since IV. joins the dorsal branch of V. on its dorsal side and separates from it on the ventral side (Fig. 3), there must be a crossing of fibres; this crossing I found clearly shown in sagittal sections of one of my older embryos. Gaupp ('97, p. 136) speaks of this relation of IV. and V. in the frog, and presumes that the branch given off to m. superior obliquus is composed of fibres from IV., but he did not actually observe the crossing of fibres.

For the study of the *abducens* (VI.), Spelerpes proved to be especially advantageous. In this species the abducens does not enter the Gas-

serian ganglion, as it does in some of the Amphibia, but (Fig. 3) comes into contact with the ventral side of r. ophthalmicus V. (*V. opt.*) a short distance anterior to its emergence from the ganglion. Owing to this condition it is much easier to follow the fibres of the two nerves in this species than in those where the two nerves emerge from the ganglion together. Herrick ('**94**, p. 200) describes for Amblystoma two branches of the sixth nerve, one of which goes to m. rectus externus, the other to m. retractor bulbi, but he thinks the branch to the latter muscle ought really to be assigned to the trigeminus, and so colors it in his figures. Although in Spelerpes the sixth lies in immediate contact with r. ophthalmicus V., yet I was able to trace its fibres with accuracy in several series of preparations, and am certain that there is no ventral branch given off from V., but that VI. divides into two branches, one (*VI. rt. ex.*) going to m. rectus externus, the other (*VI. ret. bl.*) to m. retractor bulbi. On the latter branch was found, in the region indicated by *cl. gn'*. (Pl. **2**, Figs. 3, 4), a distinct aggregation of ganglionic cells, similar to those enveloping the oculomotorius. I have found no reference to such cells connected with the sixth nerve, except in one sentence of Strong's article ('**95**, p. 134), where he says: "There seem to be ganglion cells in connection with it [abducens] (703), although these may belong to the oculomotor nerve." I have not yet tried methods to show the connection of these ganglionic cells with the nerve fibres. Only two roots were found, as in Necturus; these emerge from the ventral side of the medulla in about the same transverse plane as the most anterior roots of IX. + X.

D. Trigeminus.

(1) *Roots.* — The little study which I have hitherto given to the roots of the cranial nerves in Spelerpes has shown that there is apparently a close correspondence to the condition found by Kingsbury ('**95**.) in Necturus.

Fibres forming the trigeminus root are: (1) a large ascending bundle (Plate **1**, Fig. 2, *V. rx.*) of mostly small fibres lying ventrad to the eighth nerve, presumably the ascending tract of the fifth, though they were not traced back into the dorsal column of the spinal cord. It is possible that fibres from a sensory nidus (terminal) may be associated with these, as in Necturus; but none were distinguished; (2) two small, presumably motor, bundles of large, deeply staining fibres (*V. rx. mot.*), which arise from the floor of the metencephalon and join the ventral side of the ascending tract of the fifth, just before its exit from the brain;

(3) coarse fibres from the roof of the mesencephalon (not shown in the Figures), which curve ventrad and caudad and pass out of the brain with the other roots of the fifth. After emergence from the brain, the trigeminal fibres run obliquely cephalad and laterad, as indicated in Figures 1 and 2 (Pl. 1), and can be traced through the ventral half of the Gasserian ganglion into rami ophthalmicus, maxillaris, and mandibularis. The fibres are of medium size and in iron haematoxylin take a *grayish* blue stain, in sharp contrast to the large fibres from the seventh nerve, which take a *deep* blue stain. The latter run through the dorsal part of the ganglion, from which they emerge as r. ophthalmicus superficialis VII. and r. buccalis VII.

(2) *Branches.* — (*a*) *Ramus ophthalmicus trigemini* (Figs. 1–4, *V. opt.*) leaves the anterior mesial part of the Gasserian ganglion, runs directly cephalad, and comes in contact with III. and VI., as already (pp. 181 and 182) described. Just posterior to the eye, in the transverse plane in which the optic nerve emerges from the cartilage of the brain wall, the ophthalmicus trigemini gives off a large dorsal branch (*Va*, Figs. 1, 3, 4). From this branch arise two small branches Va^1 and Va^2 (Fig. 3). The more posterior and lateral of the two branches (Va^1) follows m. rectus superior to its insertion on the eyeball.

The other branch (Va^2) goes to the skin of the dorsum; it divides, sending one branch cephalad and another caudad. The main branch (*Va*) curves along the dorsal median surface of the eye (Figs. 1, 3, 4) in connection with IV. (Fig. 4), as previously described, and is distributed to the skin in the region in front of the eye.

Ramus opthalmicus V., after giving off the dorsal branch (*Va*) just described, takes its usual course forward, above the optic nerve (Fig. 3), close beside m. rectus internus, and divides into three branches (Figs. 1–3). The most ventral of these (*V. l. na.*) curves around in front of the eye to the skin of the external nares and cheek; it corresponds to Gaupp's r. lateralis narium. The middle one of the three branches curves ventrad and anastomoses (*coms.*) with r. palatinus VII. This condition agrees with that found by Herrick in Amblystoma. Strong ('**95**, p. 122) also finds an anastomosis of these two branches in the tadpole, but it takes place farther cephalad than in Spelerpes. The anastomosing nerves continue cephalad after their union, but could be traced only a short distance in the loose tissue in the roof of the oral cavity, just median to the internal nares. The most dorsal of the three branches (*V. m. na.*) of the ophthalmicus (Gaupp's r. medialis narium) runs above the olfactory and innervates the skin at the tip of the nose.

(*b*) *Ramus maxillaris trigemini* emerges from the Gasserian ganglion in the same transverse plane with r. buccalis and r. ophthalmicus superficialis VII., and the three appear (Fig. 2) as one nerve for a short distance, as they pass laterad and cephalad between m. temporalis and m. masseter. While ramus ophthalmicus superficialis VII. separates from the others and curves mesiad, rami maxillaris V. and buccalis VII. pass cephalad along the dorso-lateral surface of the masseter muscle. In many of the specimens examined the two appear like one nerve, but the difference in the size and distribution of the fibres was always noticeable, and in the series of sagittal sections used for reconstructions they were clearly separate. R. maxillaris (*V. mx.*) gives off a small general cutaneous branch, not shown in the drawings, to the dorsum immediately after leaving the ganglion, and its final distribution is to the skin of the cheek. It does not anastomose with ramus palatinus VII., as is the case in the tadpole of Rana (Strong).

(*c*) *Ramus mandibularis trigemini* (*V. md.*) leaves the ganglion directly below ramus maxillaris, passes ventro-laterad, gives off first a branch ($V\beta$) to m. masseter, next, two more small branches (not figured) to the same muscle, and then a fourth ($V\gamma$), which runs dorsad to m. temporalis. In the same transverse plane with $V\gamma$ there arises a cutaneous branch ($V\delta$), which runs ventro-laterad and is distributed to the skin posterior to the angle of the jaw. It comes into very close connection with the more anterior branch of ramus mandibularis externus VII.; in some series of sections it even appears to anastomose with this branch of VII.; but other sections show conclusively that it does not. Another general cutaneous branch ($V\epsilon$) is given off from ramus mandibularis V. to the angle of the jaw, a small twig from it turning caudad; the main branch ($V\epsilon$), however, runs forward, close above ramus mandibularis externus VII. to the skin of the lower lip. A division of the main nerve into nearly equal parts (*V. md. i.* and *V. md. ex.*) soon occurs. A musculo-cutaneous branch (*V. md. i.*), Gaupp's ramus mandibularis internus V., passes ventrad between os dentale and Meckel's cartilage to the lower side of the jaw, where it innervates m. mylohyoideus and the skin superficial to it. The other branch (*V. md. ex.*), which is purely cutaneous, remains on the upper side of the jaw and is distributed to the skin of the lower lip. It corresponds to Gaupp's ramus mandibularis externus V.

E. Facialis and Acusticus.

1. *Roots.* — Apparently the roots of the facial and acoustic nerves (Pl. 1, Figs. 1, 2) agree with the condition in Necturus as described by Kingsbury ('95); at least the relation of the several components as they emerge from the brain is the same. Most caudal and ventral is the motor root of the facial (*VII. rx. mot.*),* formed from two rootlets of deeply staining fibres, which arise from the median ventral region of the medulla. Dorsal to this emerges the one large root of the acoustic (*VIII. rx.*), and close to the dorsal side of the latter the fine unstained fibres of the fasciculus-communis root of the facial (*VII. rx. fas. com.*). At a little distance dorsad to these three roots and a little more cephalad emerge the very coarse, deeply staining fibres of the lateral-line root of the facial (*VII. rx. ln. l.*).† This is the "dorsal VII." of Strong. The fibres of this root are not grouped into two distinct rootlets, as in Necturus, though from the appearance of some sections there seems to be a tendency toward such a grouping. Immediately on leaving the brain the fibres of this component unite with those of the three roots ventral to it, forming a continuous dorso-ventral sheet (Fig. 1).

The dorsal root (*VII. rx. ln. l.*), however, quickly divides, and its more ventral fibres curve ventrad and laterad to enter the acustico-facialis ganglion (*gn. ac.-fac.*), while its more dorsal fibres pass directly cephalad along the mesial surface of the ear capsule in the form of a thin dorso-ventrally expanded sheet (compare Fig. 2), and enter the Gasserian ganglion.

This dorsal part of the lateral-line root of VII. contains ganglionic cells, which lie dorsal to those of the Gasserian ganglion proper, with which, however, they become fused into a common mass. Nevertheless, the fibres of this portion of the lateral-line root are clearly traceable in their passage through the Gasserian ganglion, from which they emerge as two.

2. *Branches.* — (*a*) *R. ophthalmicus superficialis* (*VII. opt. suf.*) *and* (*b*) *r. buccalis* (*VII. buc.*) *of the seventh nerve.* Both of these branches are distributed to lateral-line organs, the former giving off numerous twigs throughout the whole of its course from the ganglion to the tip of the nose. Ramus buccalis VII. has already been referred to as following closely the course of r. maxillaris V. (see Fig. 2), though

* By an oversight this is lettered in Fig. 1 as *VI. rx. mot.*

† Not lettered in Fig. 1. In this figure it is almost directly below the lettering "*rm. aur.*"

it extends farther anterior than the latter. (*c*) *The acusticus.* Three of the branches of the eighth nerve have been represented in the drawings in neutral tint, — ramulus ampullae anterioris (*rml. amp. a.*), ramulus ampullae externae (*rml. amp. ex.*), and ramulus ampullae posterioris (*rml. amp. p.*). These were plotted simply to show their relation to the seventh nerve. Fibres to the macula ac. sacculi and macula ac. neglecta were observed, but these were only slightly differentiated at the stage here reproduced. They could be clearly traced in a larva 40 mm. long. The anterior portions of VII. and VIII. remain connected with each other until after r. palatinus VII. is given off; the acoustic then curves dorsad and enters the ear capsule, while the facialis curving ventrad and ectad passes out through the cartilage of the skull.

The first of the branches to be given off from the ventral part of the facialis is the (*d*) *r. palatinus*, whose fibres are derived exclusively from the fasciculus-communis component. The ganglion of this root, lying close to the point where r. palatinus emerges, is fused with that of the eighth nerve and "represents probably the geniculate ganglion" (Kingsbury, '**95**, p. 187). The fibres of this component are always easily recognizable, since they are very fine and with iron haematoxylin take only a faint stain, or sometimes none at all. The greater portion of the fibres of the fasciculus communis goes to form this branch (r. palatinus), which passes directly cephalad, giving a few fine branches to the roof of the pharynx, and anastomosing, as already stated, with r. ophthalmicus V.

The few remaining fibres of the fasciculus communis pass out through the ventral wall of the ear capsule with the hyomandibular portion of the facialis, run through the ganglion of the lateral-line component of the facialis, which lies beneath the cephalic end of the otic capsule, and emerge as (*e*) *r. mandibularis internus VII.* (*VII. md. i.*), or *r. alveolaris VII.*, which Strong ('**95**, p. 187) homologizes with the chorda tympani of higher vertebrates. In Spelerpes this branch is very minute, and in the sagittal sections used for reconstruction could be traced only a short distance anterior to the articulation of the jaw (Figs. 1, 2); but in transverse sections it could be traced along the inside of the jaw to its termination in the ventro-lateral wall of the pharynx. It does not, in any part of its course, enter a canal, agreeing in this respect with Siren lacertina as described by Wilder ('**91**).

(*f.*) *R. mandibularis externus VII.* (*VII. md. ex.*), or *r. mentalis VII.*, the ventral part of the lateral-line component of the seventh, passes ventrad and cephalad from its ganglion, which lies under the otic capsule,

and soon divides into two nearly equal branches, both of which first run ventrad into the lower jaw, then cephalad, nearly parallel to each other, to the tip of the chin, supplying the lateral-line organs along their course. One of these (*VII. md. ex.'*) is more ventral and median than the other (*VII. md. ex.*). Strong ('**95**, p. 134) says of this branch in Amblystoma: "It is a cutaneous nerve; and probably, as in the tadpole, supplies the lateral sense organs." Its ganglion is "composed of large ganglion cells." Herrick ('**94**, p. 199), however, found no ganglion in the course of the r. mandibularis externus in Amblystoma.

Strong ('**95**, p. 163) has called attention to the fact that the r. buccalis of von Plessen und Rabinovicz is misnamed, that it corresponds to r. mandibularis externus VII., and is derived from the ventral division of the lateral [*i. e.* lateral-line] root. Apparently a further interpretation of their designations must be made, for their "Begleiter des R. hyoideo-mandibularis" (their ramus hyoideo-mandibularis and by inference its "Begleiter" are distributed to the skin of the cheek and the lower jaw) also clearly belongs to the lateral-line component. It is probable that, while their r. buccalis corresponds to one of the two branches (the more lateral, *VII. md. ex.*) of r. mandibularis externus VII. as found in Spelerpes, their "Begleiter" corresponds to the other (the more nearly median, *VII. md. ex.'*) branch.

Herrick ('**94**, p. 199), following too closely von Plessen und Rabinovicz, has repeated for Amblystoma their mistake concerning this "Begleiter." He describes the ramus buccalis and the accessory ramus hyomandibularis ("Begleiter") as following the ectal aspect of the jaw bone to the tip of the lower jaw, and as being distributed to the skin. He says: "The fibres of the ramus buccalis are mainly, if not wholly, derived from the dorsal root, as Strong has pointed out. The nerve which I have called the accessory hyomandibular seems to be the same as Strong's 'small branch to lower jaw,' which he derives from the fasciculus communis and considers the representative of the chorda tympani of higher forms." But obviously the homologue of Strong's "small branch to lower jaw" is not Herrick's accessory hyomandibular, but his r. alveolaris.

(*g.*) *R. hyomandibularis VII.* in Spelerpes is very short, as compared with its length in the tadpole. In the latter, it is prolonged, as it were, almost to the anterior margin of the eye before its first branch, r. hyoideus VII., is given off. The condition in Spelerpes corresponds more nearly to that in the adult frog. Presumably the 23 mm. larva of Spelerpes undergoes much less alteration in the course of its further development than does the tadpole, so that the two stages are not

directly comparable. Evidently the name r. hyomandibularis must be restricted in Spelerpes to the short trunk of the ventral part of the seventh, which is included between the region of its separation from the eighth and that of the giving off of r. hyoideus. Though much shorter than in the tadpole, it is made up of the same components, except that it does not embrace the general cutaneous. This constituent is represented exclusively by the communicating branch from IX. to VII. Since in Spelerpes this r. communicans IX. ad VII. is not received by the hyomandibular trunk of seven, but by r. hyoideus after its separation from the trunk (Fig. 2), it is probable * that no general cutaneous fibres are included in the hyomandibularis proper. This, however, is not a fundamental difference, being merely a question of the earlier or later accession of r. communicans to branches of the seventh. In one point, only, is a greater importance to be noted: r. mandibularis ext. in Spelerpes probably does not contain, as in the tadpole, a general cutaneous component.

The (*h*) *r. hyoideus* after receiving r. communicans from IX.+X, curves latero-ventrad and is distributed to m. digastricus and m. mylohyoideus posterior and to the skin ventral to them. The main branch (VII. *hoi.*) is figured in neutral tint, since the proportion of the two components was not accurately ascertained.

F. Glossopharyngeus and Vagus.

1. *Roots.* — The roots of this group, like those of the seventh and eighth, show apparently a close correspondence to the condition in Necturus, though a careful comparison will be necessary to determine this with certainty. The most cephalic and most dorsal root is the lateral-line component (Pl. 1, Figs. 1, 2, $IX.^{1+2}$); it resembles dorsal VII. in appearance and position. In this case, however, the root is composed of two bundles. It is equivalent to Kingsbury's $IX.^{1+2}$ and to Strong's first root of IX.+X.

The second root ($IX.^{3+4}$) emerges one section (20 μ thick) caudad and slightly ventrad of the first root; it is composed of (1) the characteristic fine colorless fibres of the fasciculus-communis component and (2) a ventral bundle, presumably motor. It corresponds to Kingsbury's $IX.^{3+4}$ and to Strong's second root.

The third root ($X.^{1}$), the equivalent of Kingsbury's $X.^{1}$, emerges

* It is of course *possible* (?) that some fibres from the r. communicans take a centripetal course in the r. hyoideus and thus reach the hyomandibular trunk of VII.

at some distance caudad of the preceding and is made up of three components: (1) most dorsal, fine fasciculus-communis fibres, (2) more ventral and caudad of fasc. com. a large bundle of coarser fibres (ascending X.), which correspond to those of ascending V., and (3), in this differing from Necturus, a ventral bundle (motor ?). The third root in the tadpole has, according to Strong, the same triple composition, but in that animal the fasciculus-communis fibres emerge ventral to those of ascending V., not cephalad of them, as in Spelerpes.

The remaining four roots are small and could not be traced in the sagittal series of the 23 mm. larva; but they were plotted on the frontal reconstruction (Fig. 2) from frontal sections of another 23 mm. specimen, and the results were checked by the study of other series of (transverse) sections. These four roots all appear to be motor, for they arise in the same horizontal plane from ventral fibres, which turn cephalad after emerging from the medulla. Kingsbury's $X.^2$, $X.^3$, and $X.^5$ are in his opinion motor, but he says that $X.^4$ is probably sensory, and that its fibres accompany those of ascending V.

2. *Branches.* — The *coarse* fibres of the first root in Spelerpes can be easily traced through the upper part of the ganglion IX.+X., and all but a few of them, which are given off dorsally (see Fig. 1, *rm. su'tp.*), pass out at the posterior end of the ganglion as the lateral-line nerves — (*a*) *ramus lateralis* — to be distributed to the lateral-line sense organs of the body.

The remaining coarse fibres form a branch (*rm. su'tp.*) which passes dorsad and ectad and divides into two small branches which innervate sense organs just posterior to the ear. Following Strong's nomenclature, this may be called (*b*) *ramus supratemporalis*, though it does not curve cephalad, as in the tadpole. It may be noted in passing that the "ectad tendency" of the cranial nerves in Spelerpes, as compared with the "cephalad tendency" in the tadpole, is a noticeable difference between the two forms, and is probably due to the more anterior position of the gills in the tadpole.

There is a bundle of general cutaneous fibres (*rm. aur.*), which leaves ganglion IX.+X. in company with r. supratemporalis, from which, however, it immediately separates and runs dorso-cephalad to the skin above the ear capsule. It corresponds in composition and distribution to the branch called by Strong (*c*) *ramus auricularis*, and known in the frog as r. cutaneus dorsalis.

From the cephalo-lateral portion of the ganglion there pass out three branches, which for a short distance are united into a single trunk. The

first branch to separate from the trunk is (*d*) *ramus communicans ad facialem* (*rm. comn.* IX.–VII.), which follows the latero-ventral surface of the ear capsule till it unites with r. hyoideus VII., as already described. Strong ('95, p. 130) gives reasons for considering this branch a general cutaneous; its relation to VII. in Spelerpes would seem to add evidence of the correctness of this view.

The second branch, (*e*) *ramus pharyngeus* (*rm. phy.*), given off from the main trunk is very small, and is composed of the fine unstained fibres of the fasciculus-communis component; it was traced to the roof of the pharynx, where fibres were seen to pass down to the end buds. This branch was traced in transverse series, and likewise in sagittal series of larger heads, as far cephalad as the separation of r. palatinus VII. from its ganglion, but in the sagittal sections of the small individual used for reconstruction it could be followed only as far as indicated in Figures 1 and 2.

The third branch of this group, (*f*) *ramus lingualis* (*IX. rm. lng.*), passes ectad, gives off a small motor branch to m. cerato-hyoideus externus, then runs ventrad to the under side of the first epibranchial bar, then curves cephalo-mesiad and is traceable in transverse sections, though not in sagittal ones, to the sense organs of the dorsum of the tongue. The fibres have the same appearance as those of all the other branches of the fasciculus-communis group.

Another branch of fasciculus-communis fibres (*g*) *ramus branchialis* (*rm. brn.*), leaves ganglion IX.+X. immediately caudad of the common trunk of the three branches last described. It appears to give some fine branches to blood-vessels soon after its emergence, but this could not be determined with certainty. The trunk soon divides; the more anterior branch goes to the first and second gills, the posterior to the third gill. It was very difficult to follow the fibres, and their distribution could not be satisfactorily worked out. Minute branches were given off during their course to the gills, but could not be traced to their terminations. A few motor twigs to gill muscles could be distinguished, as they were more deeply stained, and from the posterior branch general cutaneous fibres were seen to pass to the skin. The fine fasciculus-communis fibres were followed to the under side of the gill bars, where they lie close to large blood-vessels, but they could not be traced further. Though their ultimate distribution could not be learned, it seems to me allowable to homologize them with the rami branchiales of the tadpole. Their caudad rather than cephalad course is accounted for by the more posterior position of the gills in Spelerpes.

The last branch from the IX.+X. complex to be described is (*h*) *ramus visceralis* (*X. rm. vsc.*). It has been left in neutral tint to the point of branching, for the same reason that was given for r. hyoideus. It leaves the latero-caudal angle of the ganglion ventral to the lateral-line nerves, and curves ventrad. It is composed of deeply staining and of unstained fibres. Part of the latter are given off in the first branch (*X. rml. vsc. oe.*), which was followed caudad to the region of the oesophagus. Other branches, not plotted in the drawings, were given off mesiad from the region in which the nerve separates into two motor branches (Fig. 1). One of these motor branches (*rm. lar.*) curves cephalad, following closely the course of the hypoglossus for a short distance. It is distributed in part to a transverse sheet of muscles below the pharynx, which Wilder ('**91**, p. 188) interprets as resulting from a fusion of digastricus pharyngis and dorso-laryngeus. Spelerpes, being a lungless form, has no use for the laryngo-tracheal muscles as such. Wilder maintains that they are employed to form this pharyngo-oesophageal sheet. The distribution of the remaining portion of this branch is to the constrictor arcuum branchiarum. This branch would therefore seem to be r. laryngeus, although it issues from the ganglion with r. visceralis.

The other motor branch (*rm. scap.?*) was traced caudo-ventrad to the region of the shoulder girdle, and is perhaps the r. scapularis of Fürbringer.

G. First and Second Spinal Nerves.

(1) The *first spinal nerve* in Spelerpes bilineatus arises by two ventral roots, which run cephalad a short distance after they emerge from the brain, then pass through the cranial cartilage and divide into two branches, — a dorsal (*rm. d.* $spi._1$), which goes to m. longissimus dorsi, and a ventral (*rm. v.* $spi._1$), which curves caudad, ectad, and then ventrad, finally coming into such close relation with the hypoglossus that the two appear, even when cut transversely, as one nerve. The two remain together for a short distance, then the first spinal curves mesiad and cephalad; it was traced to the mesial surface of m. sterno-hyoideus, but fibres were not seen to actually enter that muscle.

(2) The *second spinal nerve* was found to have a ventral root (*rx. v.* $spi._2$) similar to that of the first, and also a well-developed dorsal root (*rx. d.* $spi._2$). Kingsbury ('**95**, p. 149) says, "The *hypoglossus* in Amphibia is generally described as formed by the union of the ventral trunks of the two nerves arising immediately caudad of the vagus group, to

which dorsal roots are wanting." He refers, however, to the fact that an indication of a dorsal root for the first spinal was found by Kingsley ('**92**, p. 678) in Amphiuma and by Mrs. Gage ('**93**, p. 275) in the larva of Diemyctylus.

In Spelerpes the two roots of the second spinal nerve unite into a ganglion, from which were traced a dorsal (*rm. d.* $spi._2$) and a ventral branch (*h'gls.*). The former has been represented as entirely motor, because no general cutaneous fibres were actually demonstrated, although the nerve could always be followed to the narrow space between the dorsal muscles and the overlying skin. The ventral branch is the hypoglossus nerve, which runs cephalad and supplies m. sternohyoideus and m. genio-hyoideus.

Von Plessen und Rabinovicz ('**91**, p. 20) describe the hypoglossus in Salamandra as a branch of the first cervical. No dorsal root was found, but they describe and figure a ganglion connected with the dorsal branch. Kingsley ('**92**, p. 678) mentions the persistence of the dorsal ganglion as a noticeable feature in connection with the twelfth nerve.

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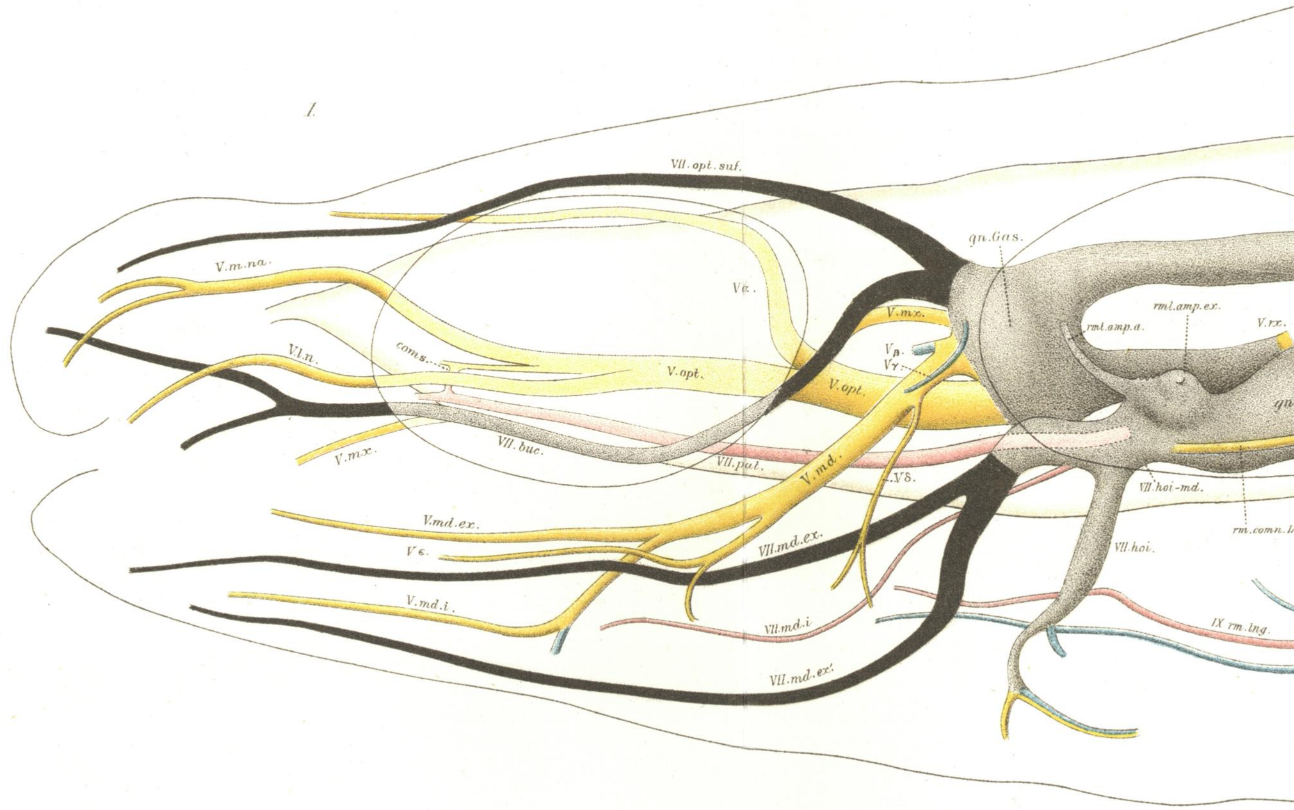
1.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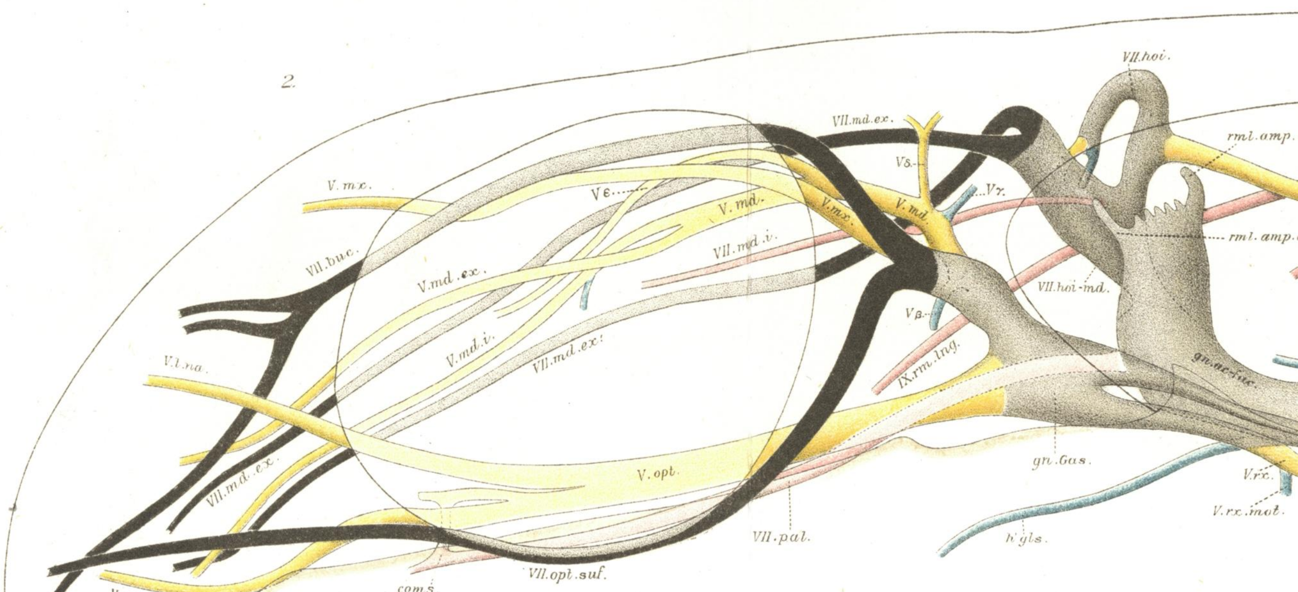
V.m.na.
Vε.
gn.Gas.
rml.amp.ex.
rml.amp.a.
V.rx.
V.mx.
Vl.n.
coms.
V.opt.
Vβ.
Vγ.
V.opt.
V.mx.
VII. buc.
VII. pal.
V.md.
Vδ.
VII. hoi-md.
V.md.ex.
Vε.
VII.md.ex.
VII. hoi.
V.md.i.
VII.md.i
IX rm.lng.
VII.md.ex.

2.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VII.buc.
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V.md.ex.
VII.hoi-md.
Vβ.
V.md.i.
VII.md.ex.
V.l.na.
IX.rm.lng.
gn.Gas.
V.opt.
V.rx.
VII.md.ex.
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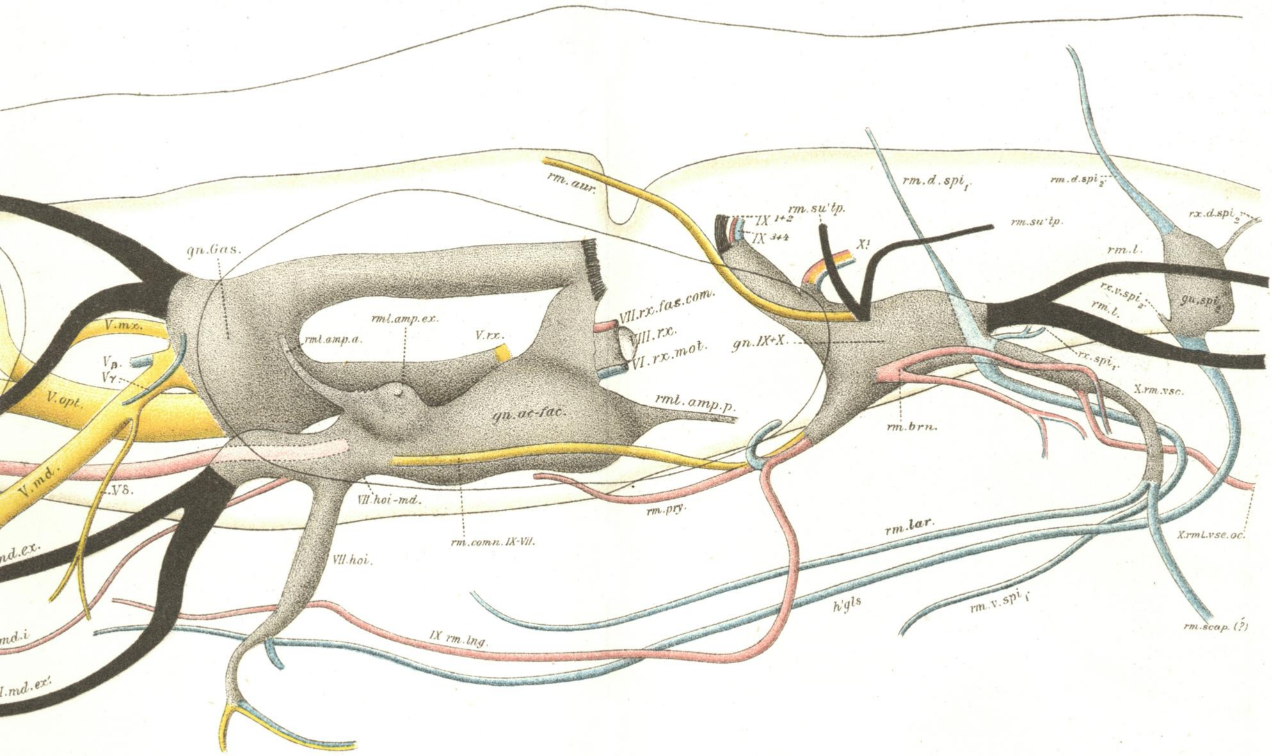
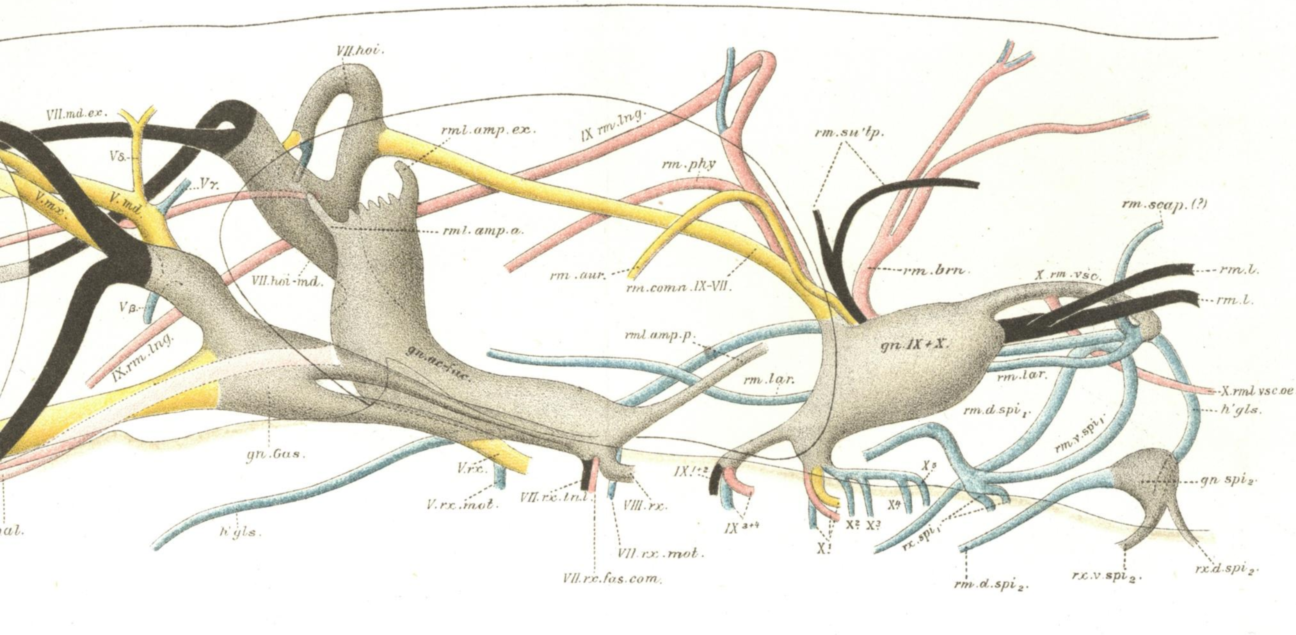
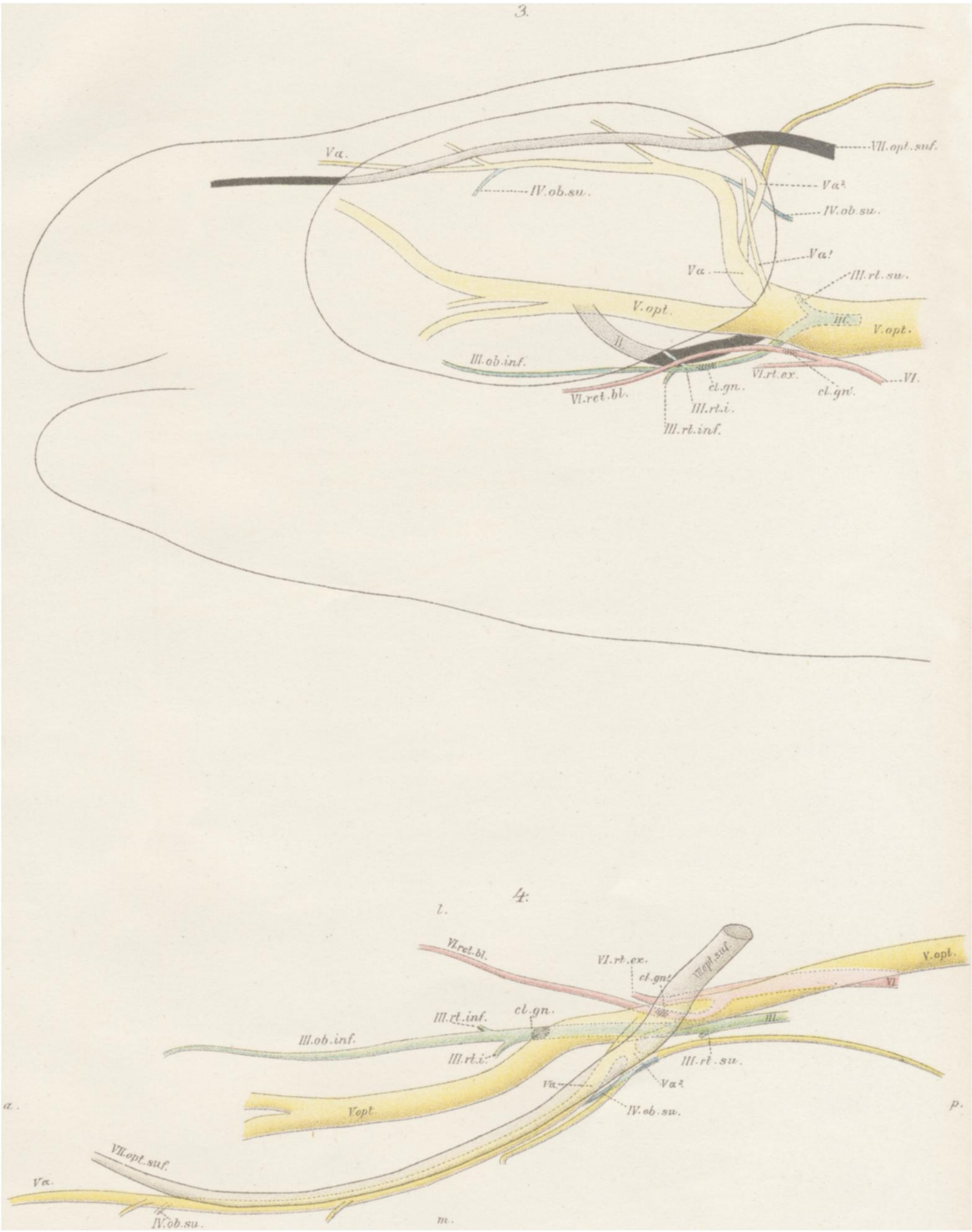
VII.pal.
h'gls.
coms.
VII.opt.suf.
V.m.na.

M.A.B. del.





B. Meisel, lith. Boston.


3.
VII.opt.suf.
Va.
IV.ob.su.
Va²
IV.ob.su.
Va!
Va.
III.rt.su.
V.opt.
III.
V.opt.
II
III.ob.inf.
VI.rt.ex.
VI.
cl.gn.
cl.gn!
VI.ret.bl.
III.rt.i.
III.rt.inf.
4.
l.
VI.ret.bl.
VI.rt.ex.
cl.gn.
VII.opt.suf.
V.opt.
VI.
III.rt.inf.
cl.gn.
III.
III.ob.inf.
III.rt.i.
III.rt.su.
Va.
Va²
a.
V.opt.
IV.ob.su.
p.
VII.opt.suf.
Va.
IV.ob.su.
m.

EXPLANATION OF PLATES.

All figures are reconstruction drawings from sagittal sections of *Spelerpes bilineatus*.

The colors employed follow the scheme adopted by Strong, viz.:

Black for lateral line (also for optic n.),	Pink for fasciculus communis,
Yellow for general cutaneous,	Blue for motor.

List of Abbreviations.

II.	Opticus.
III.	Oculomotorius
III. ob. inf. . .	Branch of III. to m. obliquus inferior.
III. rt. i. . . .	" " " rectus internus.
III. rt. inf. . . .	" " " " inferior.
III. rt. su. . . .	" " " " superior.
IV. ob. su. . . .	Trochlearis to m. obliquus superior.
Vα	Dorsal branch from ophthalmicus trigemini.
Vα[1]	Small branch of *Vα*. (follows m. rectus superior).
Vα[2]	" " " (to skin of dorsum).
Vβ	Branch of r. mandibularis *V*. (to m. masseter).
Vγ	" " " " (to m. temporalis).
Vδ	" " " " (to skin posterior to angle of jaw).
Vε	" " " " (to skin of lower lip).
V. l. n.	Erroneously engraved in Fig. 1 for *V. l. na.*
V. l. na.	Ramus lateralis narium.
V. m. na. . . .	" medialis "
V. md.	" mandibularis trigemini.
V. md. ex. . . .	" " " externus trigemini.
V. md. i. . . .	" " " internus "
V. mx.	" maxillaris trigemini.
V. opt.	" ophthalmicus trigemini.
V. rx.	Ascending root of the trigeminus.
V. rx. mot. . . .	Motor " " "
VI.	Abducens.
VI. ret. bl. . . .	Branch of VI. to m. retractor bulbi.
VI. rt. ex. . . .	" " " rectus externus.
VI. rx. mot. . .	Erroneously engraved in Fig. 1 for *VII. rx. mot.*
VII. buc. . . .	Ramus buccalis facialis.
VII. hoi. . . .	" hyoideus "
VII. hoi-md. . .	" hyomandibularis facialis.
VII. md. ex. . .	Branch of ramus mandibularis externus (or mentalis) facialis.
VII. md. ex.′ . .	" " " " " " " "

EXPLANATION OF PLATES.

VII. md. i. . .	Ramus mandibularis internus (or alveolaris) facialis.
VII. opt. suf. . .	" ophthalmicus superficialis facialis.
VII. pal. . . .	" palatinus facialis.
VII. rx. fas. com.	Fasciculus-communis root of the facialis.
VII. rx. ln. l. . .	Lateral-line root of the facialis.
VII. rx. mot. . .	Motor root of the facialis.
VIII. rx. . . .	Root of auditory nerve.
IX^{1+2}	Anterior root of the ninth cranial nerve.
IX^{3+4}	Posterior " " " "
IX. rm. lng. . .	Ramus lingualis glossopharyngei.
$X^1 - X^5$ . . .	Roots of the tenth cranial nerve.
X. rml. vsc. oe. .	Branch of visceralis vagi to the oesophagus.
X. rml. vse. oc. .	Erroneously engraved in Fig. 1 for *X. rml. vsc. oe.*
X. rm. vsc. . . .	Ramus visceralis vagi.
a.	Anterior.
cl. gn.	Ganglionic cells of oculomotorius.
cl. gn.′	" " " abducens.
coms.	Commissure between the r. palatinus VII. and the r. ophthalmicus V.
gn. IX. + X. . .	Ganglion of the glossopharyngeus and the vagus nerves.
gn. ac-fac. . . .	Ganglion acustico-facialis.
gn. Gas.	Gasserian ganglion.
$gn.\ spi._2$	Ganglion of second spinal nerve.
h'gls.	Hypoglossus nerve.
l.	Lateral.
m.	Median.
p.	Posterior.
rm. aur.	Ramus auricularis.
rm. brn.	" branchialis.
rm. comn. IX.-VII.	" communicans glossopharyngei ad facialem.
$rm.\ d.\ spi._1$ . . .	Dorsal branch of first spinal. NOTE. — In Fig. 2 the dotted line has been omitted; it should have run to the left and downward from the letters *rm.*
$rm.\ d.\ spi._2$ . . .	Dorsal branch of second spinal.
rm. l.	Ramus lateralis.
rml. amp. a. . .	Ramulus ampullae anterioris.
rml. amp. ex. . .	" " externae.
rml. amp. p. . .	" " posterioris.
rm. lar.	" laryngeus.
rm. phy.	" pharyngeus.
rm. pry.	Erroneously engraved in Fig. 1 for *rm. phy.*
rm. scap. (?) . .	Ramus scapularis (?).
rm. su'tp. . . .	" supratemporalis.
$rm.\ v.\ spi._1$ . . .	Ventral branch of first spinal.
$rx.\ d.\ spi._2$ . . .	Dorsal root of second spinal.
$rx.\ spi._1$	Root of first spinal.
$rx.\ v.\ spi._2$ . . .	Ventral root of second spinal.

For the sake of convenience in comparing Fig. 1 with Fig. 3, and Fig. 2 with Fig. 4, Plates 1 and 2 have been bound in *facing* each other.

PLATE 1.

FIG. 1. View of the roots, ganglia, and branches of the cranial nerves of the left half of the head, as if seen from the left side projected on to the sagittal plane. The ear capsule and the eyeball are represented in outline, and the contour of the brain by a line accompanied by a tint on one side of it. × 72.

FIG. 2. Dorsal aspect of the roots, ganglia, and branches of the cranial nerves of the *right* half of the head projected on to the frontal plane. The drawings were made from reconstructions of the *left* half of the head, but in engraving were reversed for the sake of readier comparison with Fig. 4. Outlines of eye, ear, and brain represented as in Fig. 1. × 72.

PLATE 2.

FIG. 3. View of the branches of the cranial nerves in the vicinity of the left eye, seen from the left side, projected on to the median plane, to show especially the eye-muscle nerves in relation to the II. and certain branches of the V. and VII. cranial nerves. × 72.

FIG. 4. Dorsal view of the nerves shown in Fig. 3, but from the *right* side of the head, projected on to the frontal plane. Compare also with Fig. 2. The superficial ophthalmic VII. has been only faintly shaded, instead of being printed in black, in order to allow the course of the underlying nerves to be seen. The distal end of *IV. ob. su.* has not been colored blue, owing to a mistake of the lithographer. × 163.